MONOGRAPH OF
THE MICRORHIZAE, DIOCIENAEAE AND ACROSTYLEAE

(GIGARTINALES, RHODOPHYTA)

by

Gerald Thompson Kraft, B.A., N.Sc.

Department of Botany, University of Adelaide

Thesis submitted to the University of Adelaide
for the degree of Doctor of Philosophy.

April, 1974.
SUMMARY

The vegetative and reproductive morphology of 21 species of three families - the Hylochoeaceae, Dicranaceae and Acrotylaceae (Gigartinales, Rhodophyta) - have been studied. With one exception, all are endemic to southern Australia.

The Myphodaceae contains the two genera Myphodes Hook. & Harv. and Neurophyllis Zan., which are separated on tetrasporangial features. Sexual reproduction is uniform throughout the group.

Two species of Myphodes (M. carnose Hook. & Harv., and M. gracilae (Sond.) comb. nov.) are recognized. Both have tetrasporangia intercalary in the cortical filaments. Other species previously placed in Myphodes are shown to initiate tetrasporangia by oblique divisions of outer cortical cells, and are transferred to Neurophyllis, based on N. australis Zan. The species include

M. margicifera (Aresch.) comb. nov., N. acinulata (J. Ag.) comb. nov.,
N. pusilla (Harv.) comb. nov., N. acinulifera (J. Ag.) comb. nov.,
N. basata (Harv.) comb. nov., N. disticha (Harv.) comb. nov.,
N. ramulosa (J. Ag.) comb. nov., and N. acanthymenia sp. nov.

Algae of the Myphodaceae are uniaxial with a characteristic pattern of development, monocious, zonately tetrasporangiate, procarpic and polycarposporous. They lack fusion cells and possess multiple, filamentous gonioblast initials which develop mostly towards the thallus interior. Carposporangia arise both from gonioblast filaments and from vegetative cells in, and distant
from contact with gonimoblast filaments.

A new family, the Mychodesophyllaceae, is created for

*Mychodesophyllum papilliforme* gen. et sp. nov. *Mychodesophyllum*

shares spermatangial and tetrasporangial features with *Mychodes*,

and also sexual elements such as polycarpogonal procarps, lack

of fusion cells, and multiple, inwardly growing gonimoblast

initials. Gonimoblast filaments develop very differently, however,

and carposporangia form radiating chains around the periphery of a

central placenta from gonimoblast filaments secondarily connected

to vegetative cells. The species is also apparently multiaxial.

The Dicranemaceae contains *Dicranema revoluta* (C. Ag.) J. Ag.,

*D. cincinnati* sp. nov., *Peltata australis* J. Ag., and *Tylopus

obtusatus* (Sond.) J. Ag. The genera are distinguished on habit,

presence or absence of procarps, direction of gonimoblast develop-

ment, and morphology of the mature carposporophyte. Thalli are

multiaxial, monoecious, zonately tetrasporangiate and monocarpo-

gonal. Fusion cells form and issue multiple gonimoblast initials.

The carposporophyte is a broadly-based hemispherical placenta of

interconnected gonimoblast and vegetative tissue producing a

surface layer of carposporangia. Distinct ostioles are present.

The Acrotylaceae includes *Acrotylus australis* J. Ag.,

*Kennedyra crispis* Harv., *Reinholdia polycarpa* Schmitz, *Amphiplexia

hymenocladioides* J. Ag., and *A. racemosa* (J. Ag.) comb. nov.

The genera are very distinct in habit and vegetative structure,

and differ in whether they are mono- or polycarpogonal, have
inward or outward gonimoblast development, and in the form of the carposporangial filaments. Thalli are multiaxial, usually monoeccious, monoeccially tetrasporangiate, and possess multiple gonimoblast initials which produce filaments that enter or line a pericarp of nutritive cells surrounding a cavity and give rise to carposporangial filaments growing centripetally into the cavity. Fusion cells are lacking and ostioles are present in the genera.

Distinctions between the families studied are based largely on features of gonimoblast initiation and early growth, but primarily on the origin of carposporangial cells or filaments. Other features, such as type of axis (uni-, or multiaxial), spermatangial and tetrasporangial development, number and shape of carposporangial branches, presence or absence of procarps, fusion cells and ostioles, and the direction of gonimoblast growth, are either used as supporting evidence for family groupings or are found too variable among related genera to warrant major emphasis.

In the Nychodeaceae, carposporangia arise from gonimoblast filaments and on vegetative cells throughout the cystocarp and are secondarily linked to form irregular, intercalary chains. In the Nychodeophyllaceae, chains of carposporangia radiate from a central placenta where gonimoblast filaments are secondarily connected to vegetative cells. In the Dicranemaceae, single carposporangia form on filaments covering the surface of a hemispherical placenta of interconnected vegetative cells and gonimoblast filaments derived from a characteristic type of
fusion cell. In the Acrotylales, carposporangial filaments grow centripetally into a hollow chamber from a pericarp of intermixed gametoblast and nutritive cells.

Early germination stages of carposporangia have been studied in culture for a member of each family (except the Mychodeophyllales) and are very similar. Thalli of one species of Mychodes and one of Neurophyllis have been reared over two years and their growth patterns studied.

It is concluded that the families Mychodesaceae, Mychodeophyllales and Acrotylaeaceae show probable links to members of the Solieriaceae and Rhodophyllidaceae. The antecedents of the Dicranemales are not clear, but may best be sought in the Sarcodiaceae.
CONTENTS

ACKNOWLEDGEMENTS ................................................. ii
SUMMARY ................................................................ iv
I. INTRODUCTION ......................................................... 1
II. MATERIALS AND METHODS ...................................... 4
III. DESCRIPTION OF TAXA .......................................... 6
Key to Families of Gigartinales Studied ......................... 6
A. Family MICRODAEACEAE Kylin ...................... 7
   Key to the Genera of the Mychodesaceae and
   Mychodeophyllaceae ............................................ 9
   Key to the Species of the Mychodesaceae and
   Mychodeophyllaceae ............................................ 9
1. Genus MYCHODA Hooker & Harvey .................. 12
   N. carnea Hooker & Harvey .............................. 15
   N. gracilis (Sonder) comb. nov. ....................... 26
2. Genera NEUROPHYLLES Zanardini and
   ECTOCLINUM J. Agardh ................................... 32
   N. australis Zanardini ..................................... 34
   N. ramulosa (J. Agardh) comb. nov. .................. 41
   N. pusilla (Harvey) comb. nov. ...................... 46
   N. spiculifera (J. Agardh) comb. nov. ............... 52
   N. acicularis (J. Agardh) comb. nov. ............... 55
   N. disticha (Harvey) comb. nov. ..................... 63
   N. haecke (Harvey) comb. nov. ....................... 69
   N. marginifera (Areschoung) comb. nov. .......... 73
   N. acanthomenia sp. nov. ............................... 81
Species Removed from the Mychodesaceae ............... 86
DISCUSSION OF THE MICRODAEACEAE ................... 93
B. Family MICRODOPHYLLACEAE fam. nov. .......................... 99

Mycophyllum papillilectum gen. et sp. nov. .............. 101

DISCUSSION OF THE MICRODOPHYLLACEAE .................... 107

C. Family DICRANEMACEAE Kylin .................................. 109

Key to the Genera and Species of the Dicranemaceae ... 111

1. Genus DICRANUM Sonder .......................................... 113

D. revolutum (C. Agardh) J.Agardh ......................... 115

D. ciscinialis sp. nov. ........................................... 123

Excluded and Doubtful Species of Dicranum ............. 129

2. Genus PELTASTA J. Agardh ............................... 136

P. australis J. Agardh ........................................ 137

3. Genus TILLOTUS J. Agardh ................................. 144

T. obtusatus (Sonder) J. Agardh ......................... 146

Possible but Uncertain Species of Tylophora ........ 154

Species Removed from Tylophora .......................... 155

DISCUSSION OF THE DICRANEMACEAE ......................... 159

D. Family ACROTYLACEAE Schmids & Hauptfleisch .......... 162

Key to the Genera and Species of the Acrotylaciae .... 163

1. Genus ACROTYLUS J. Agardh ........................... 165

A. australis J. Agardh ...................................... 166

Species Removed from Acrotylus ......................... 173
2. Genus REINHOLDIA Schmitz .......................... 174
   R. polyacra Schmitz in Schmitz & Hauptfleisch. 175
3. Genus NEUENHEIA Harvey ........................... 180
   H. cripa Harvey .............................. 181
4. Genera BINDERIA, BINDERIELLA and AMPHIPLEXIA .... 188
   A. hymenocladioides J. Agardh .................... 191
   A. racemosa (J. Agardh) comb. nov. ............... 197
   Discussion of Amphiplexia ........................ 201

DISCUSSION OF THE ACROTIACEAE .......................... 202

IV. GENERAL DISCUSSION .................................. 204

V. BIBLIOGRAPHY ......................................... 211

Abbreviations Used in Figures

Figures 1-82
I. INTRODUCTION

Knowledge of red algae in the order Gigartinales has advanced greatly in recent years through detailed morphological studies of several of its families (e.g. J. Feldmann 1934, Mikasa 1965, Min-Thein 1973, Searles 1968, Schottler 1968). The criteria by which most of the twenty or so families of the order are distinguished are still largely those set down by Kylin (1956, p. 238). The features of greatest significance in Kylin's system are: a) whether the gonimoblast grows from the auxiliary cell towards the center of the thallus or towards the surface; b) whether several, or only a single, gonimoblast filaments are initiated by the diploidized auxiliary cell; c) whether chains of several, or only single, carposporangia are formed at the ends of sperogenous filaments; d) whether thalli are uniaxial (i.e. derived ultimately from a single apical cell) or multiaxial (i.e. the product of several, equally dividing apical cells); and e) whether the tetrasporangia are cruciately or soriately divided. Studies since Kylin's time, however, have given rise to doubts about the importance of many of his characters (cf. Searles 1968, Min-Thein 1973) and have pointed up the need for further work on some of the remaining, less understood, families.

Another continuing field of interest concerns the relationships of the gigartinalean algae to those of the Cryptosporiales, an order distinct from the Gigartinales on the single feature of whether the auxiliary cell is intercalary in an accessory (Cryptosporiales) or normal vegetative (Gigartinales) branch system (Kylin 1925, p. 39).
Some authors have thought this to be a trivial ground for separating orders (e.g. Britsch 1944, p. 265; 1945, p. 656; Drew 1957, p. 114), but if the feature is truly unimportant, one would expect that with expanding knowledge, clear interrelationships ought to emerge between various families of the two, presumably artificially separated, orders.

The detailed work done thus far on the Gigartinales and on the families of the Cryptonemiales (e.g. Abbott 1968, Chiang 1970, Kawabata 1962, Kylin 1928, 1930, Norris 1957) has not shown Kylin's ordinal criterion to be inadequate in any clearcut fashion. The distinction between the Cryptonemiales and Gigartinales continues to be generally accepted (Papenfuss 1966, Sears 1968).

The purpose of this thesis has been to select some families in the Gigartinales for detailed study which might also be expected to show clear links to previously-studied groups in the Cryptonemiales. Towards this goal, the Myxodemataceae seemed an ideal topic, for a number of features illustrated for the family in the only previous work (Kylin 1932) are similar to those described in the Kallymeniaceae (Cryptonemiales) by Norris (1957) and Hommersand & Ott (1971). These features include polycarpogonial supporting cells which become generative auxiliary cells through direct connection with a fertilized carpospogonium, multiple gonimoblast initials directed mostly towards the center of the thallus, and complex carposporophytes consisting of seeming mixtures of vegetative and gonimoblast filaments.
Two other small families, the Dicranemaceae and the Acrotylaceae, were grouped with the Myxodaceae by Kylin (1932, 1956). Since all these families are virtually confined to southern Australia, it was natural to include them in the study.

The three families, Myxodaceae, Dicranemaceae and Acrotylaceae, were thought (Kylin 1956) to form a distinctive group in the Gigartinales, along with the families Gigartiniaceae and Phyllophoraceae. All five families exhibit highly condensed procarps where the supporting cell fuses directly with the carpogonite and becomes the generative auxiliary cell. The auxiliary cells issue multiple gonimoblast initials as arms and chains of cells directed towards the center of the thallus. These features alone serve to isolate them from the rest of the order. The Myxodaceae, Dicranemaceae and Acrotylaceae are distinguished from the Gigartiniaceae-Phyllophoraceae in Kylin's system in having polycarpogonial supporting cells and being zonately, rather than cruciately, tetradsporangiate. The Myxodaceae is also distinct among the 5 families in being uniaxial, while the multiaxial Dicranemaceae and Acrotylaceae are separated on vegetative features and the shape of the carpogonophyte.